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Effects of predation risk and temperature on foraging behaviour of *Littorina* littorea

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Abstract

Predator-prey interactions are a fundamental feature of ecological communities. The majority of studies have focussed on the consequences of predators reducing the abundance of their prey through direct consumption (density-mediated interaction, DMIs). However, predators can also interact with prey by inducing costly behavioural and/or physiological defence strategies such as reduced foraging, anti-predator behaviour and investment in defensive structures. Evidence suggests that the cost of these phenotypic responses, termed trait-mediated interactions (TMIs), may be greater than that of DMIs. The strength of TMIs may depend on the environmental context in which prey must decide between food and safety. Because temperature can alter metabolic and foraging rates, particularly in ectotherms, this additional physiological stress may determine how prey balance this trade-off. Observations were made of the effect of predator cues and temperature on the foraging behaviour of the intertidal snail, *Littorina littorea* Both temperature and predation cue had independent effects on the amount of *Ulva lactuca* consumed, although there was no interaction between these factors. The addition of predation cue water caused *L. littorea* to consume 77% less *Ulva* compared to control treatments whereas the increased temperature resulted in 2.5 times more *Ulva* being consumed.

The results suggest that non-consumptive effects can play an important role in shaping intertidal communities and that the effects of warming may result in intertidal consumers trading energy gain for safety when under predation risk. Understanding the direct and indirect effects of temperature and predation risk on species interactions will provide greater insights into prey dynamics and cascading trophic interactions.

Introduction

In any given ecosystem, species exist within a community of other potentially interacting species. Each species within this community consumes resources and is itself consumed by other species. This predator-prey interaction is the fundamental building block from which complex food webs and food chains can be constructed (Mittelbach 2012). Studies of the effects predator-prey interactions have on community composition have been heavily influenced by the work of Paine (1966). He illustrated how the removal of predatory starfish, *Pisaster ochraceus*, which preys upon the mussel *Mytilus californicus*, resulted in a dramatic decline in species diversity on the rocky shores of Makah Bay. The bay's rocky intertidal zone normally hosts a community of mussels, barnacles, algae, and limpets. Removing the predatory starfish increased the abundance of the competitively dominant mussel, which crowded out the co-existing species, resulting in a negative indirect effect on the abundance of barnacles, algae and limpets. Within a year the habitat became a monoculture of mussels. This study was the foundation of the trophic cascade concept, which now supports an abundance of literature. A trophic cascade occurs when top predators control the density or alter the behaviour of their prey, resulting in an increase of lower trophic levels (Pace et al. 1999). Cascades are widespread, occurring in a range of latitudes from the poles to the tropics, and across a variety of ecosystems including terrestrial (Halaj & Wise 2002), freshwater (Carpenter et al. 2001) and marine (Estes & Duggins 1995). Furthermore, cascades have been shown to radiate through up to four trophic levels (Power 1990; Sitvarin et al. 2016). The majority of trophic cascade studies have focussed on the consequences of predators directly consuming their prey, known as density mediated interactions, ('DMIs',-) (Preisser et al. 2005; Trussell et al. 2008). However, evidence suggests that trophic cascades are not soley driven by DMIs. Predators can also have strong effects on their prey without consuming them by eliciting a fear response (Brown et al. 1999) known as trait-mediated interactions, ('TMIs',-). TMIs can induce phenotypic plasticity in prey and prey frequently respond to predation risk by modifying traits such as behaviour (Preisser & Bolnick 2008), morphology, and life history (Preisser et al. 2005; Okuyama and Bolker 2007; Mowles et al. 2011; Trussell et al. 2011; Paterson et al. 2013). This often has significant trade-off costs that can reduce prey fecunditiy or survival (Lima & Dill 1990; Turner 1996; Trussell et al. 2003). Non-consumptive effects are therefore receiving growing interest, as these types of predator-prey interactions often outweigh the effects of DMIs and can play a vital role in trophic cascades (Schmitz et al. 2004; Trussell et al. 2004), competitive interactions (Peacor & Werner 2001) and ecosystem function (Schmitz et al. 2008).

Littorinid snails are marine gastropods that are important herbivorous grazers in intertidal communities, which can significantly affect the density of seaweeds (Lubchenco 1978). It is widely recognised that DMIs, such as predation by crabs, are one of the principle mechanisms driving the structure of rocky intertidal assemblages through the regulation of *Littorinid* densities, and the cascading indirect impact on the densities of primary producers (Menge et al. 1997). However, more recent experiments have demonstrated that non-consumptive effects, in the form of predatory crab cues, can suppress foraging by *Littorinid* snails which in turn, causes positive indirect effects on the abundance of algal communities (*e.g.* Trussell et al. 2002). Therefore, TMIs may be an important element of assemblage composition on rocky intertidal shores. These types of predator-prey interactions may be further shaped by environmental and physiological conditions that can alter relative costs and benefits

of foraging. For example, TMIs may have more influence on foraging behaviour in resource rich systems as where prey can increase their energy reserves and reduce the risk of starvation, they are more likely to be risk adverse (McNamara & Houston 1987; Luttbeg et al. 2003). When predation risk is high, it can increase the production of stress hormones, heat shock proteins and antioxidant enzymes (Miller et al. 2014). Additionally, it can reduce prey foraging activity and increase the use of refuge habitats, resulting in a trade-off between energy gain and safety from predation, known as the growth-predation risk trade-off (Trussell et al. 2011).

The effects of predation risk on prey physiology may limit the ability of prey to cope with additional physiological stress caused by environmental factors, such as an increase in temperature. This can affect how prey balance this trade-off, especially if environmental stressors and predation risk are combined (Miller et al. 2014). Changing temperature is one of the key environmental drivers that can have widespread consequences. It influences metabolic rates and can affect nearly all species interactions, impacting on ecosystem function and population dynamics (Petchey et al. 1999; Sentis et al. 2016). The energetic demands and foraging rates of ectotherms, such as *Littorinid* snails, can often be influenced by the physiological effects of temperature (Hochachka & Somero 2002), which can cause challenges for these prey when balancing the growth-predation risk trade off (Rall et al. 2012). Increases in temperature can result in higher resting metabolic rates, increasing energy required by prey for survival or maintenance and, in turn, decreasing energy reserves and increasing foraging rates (O'Connor 2009). This can make prey more conspicuous to potential predators as well as limit their ability to trade-off food for safety. (Lima & Dill 1990; Dell et al. 2014; Matassa & Trussell 2014). Rises in metabolic demands due to increasing temperatures may exceed increased foraging rates thereby limiting prey growth (Matassa & Trussell 2014). Therefore, increased temperatures may compound the growth costs associated with reductions in foraging caused by TMIs. Consequently, temperature may be an important factor in prey foraging decisions when under predation risk, and may indirectly influence community structure through cascading effects.

In this study, my laboratory experiments examined how temperature might modify the effects of risk-induced foraging in *L. littorea.* My food chain consisted of a basal resource (the marine alga, *Ulva lactuca*), a common herbivore (the intertidal gastropod, *Littorina littorea* and chemical risk cues from a major predator of *L. littorea* (the shore crab, *Carcinus maenas*).

I predicted that an increase in temperature will alter the foraging behaviour of *L. littorea* when under threat of predation, causing them to trade-off energy gain for safety from predation.

Methodology

Study species

Throughout the experiment, all animal work was carried out in accordance with the ASAB/ABS ethical guidelines (ASAB, 2012). This work involved invertebrate species which require no research permits or approval in the UK.

I collected *L. littorea and Ulva* in September from Mt Batten, Plymouth (50˚21'28".9 N, 4˚07'39".3 W). All *L. littorea* were measured prior to the experiments (average width

17.54 mm; range 15.1-20.1 mm) and maintained on *Ulva* in six separate aquaria split between two constant temperature rooms (10°C and 20°C). Shore crabs (*C. maenas*) were collected from Mt Batten and maintained on a diet of *L. littorea* at 15°C. Overall, five crabs were used to prepare the predation cue water. All the crabs were undamaged and of medium size (average width 46.12 mm; range 39-57.2 mm). Throughout the experiment all study organisms were maintained in aerated seawater (35 PSU).

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Experiment

Two hundred *L. littorea* were food deprived for 24 hours then randomly assigned to one of two treatments: (control (seawater), or predation cue). Acetate grids were placed in the bottom of each circular dish (160 mm in diameter) and an individual snail was randomly placed into the dish filled with 600 ml of seawater. The position of each treatment and species was randomised between dishes. At the start of each trial a disc of *Ulva* (diameter 25.9 mm, area 527.85 mm^2) was placed in the centre of each dish and 60 ml of control water or predation cue water was added. Predation cue water was taken from an aquarium containing 3,200 ml of seawater in which one *C. maenas* had been maintained for 24 hrs. Due to unexpected mortalities of *C. maenas* during the first 75 trials, two smaller *C. maenas* were used to prepare cue water for the remaining 125 trails. However, Paterson et al. (2013) showed that predator cue experiments are robust in terms of experimental design and different methodologies used in these type of experiments have no impact on effect size. *Carcinus maenas* were fed two *L. littorea* at the start of the 24 hr period and two additional *L. littorea* were added to the tank immediately prior to the trials. This preparation ensured *L. littorea* were exposed to chemical cues from natural predators, and death kairomones from crushed conspecifics, a mixture which has been shown to maximise anti-predator behaviour (Cotton et al. 2004; Mowles et al. 2011).

Behavioural data were collected by scan sampling at 15 minute intervals for the first 150 minutes of each trial. Behaviour was recorded as moving, eating, stationary, at waterline or out of the water. Jacobsen & Stabell (1999), Keppel & Scrosati (2003) and Dalesman et al. (2007) have shown that crawling out of the water and avoiding predator cue water are anti-predator behaviours performmed by gastropods. To determine the overall amount of foraging, *Ulva* discs were removed after 24 hrs, placed between a sheet of graph paper and clear acetate, and then scanned into ImageJ. The area (mm^2) of the remaining *Ulva* was then calculated.

Statistical analysis

Statistical analyses were performed using R version 3.2.4 (R Core Team 2016). Because of zero inflation, all data were analysed using a quasi-Poisson generalised linear model (GLM). Pairwise comparisons among temperatures within each treatment type were examined using Tukey HSD post hoc tests.

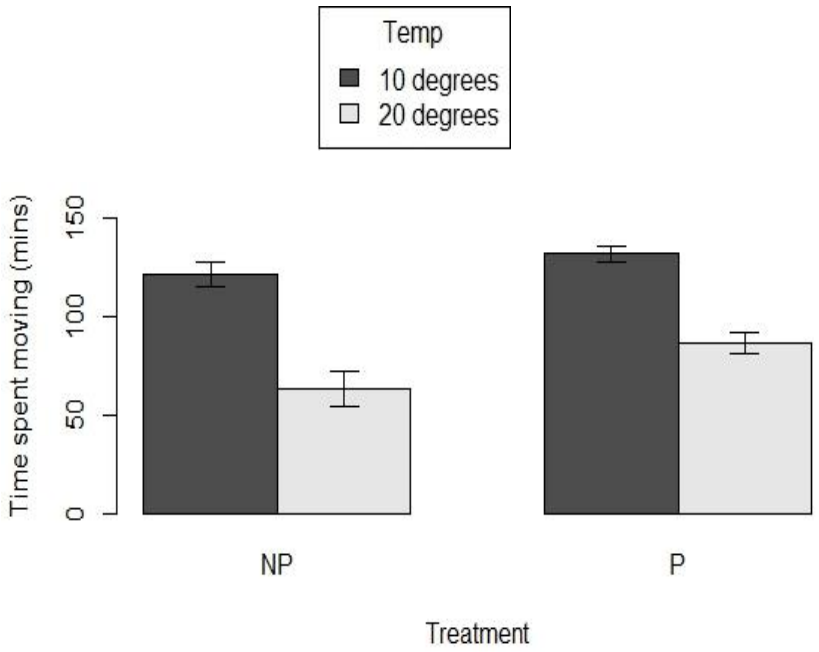
Results

Temperature had a significant effect on the amount of time *L. littorea* spent moving (t=-4.976, df=196, p=<0.0001) and remained stationary (t=4.41, df=196, p<0.0001) (Table 1). *L. littorea* assigned to 20°C remained stationary for an average of 48 minutes during the observed period compared to individuals observed at 10°C who remained stationary for an average 15 minutes. In comparison, *L. littorina* spent an average of 75 minutes moving at 20°C compared to 127 minutes at 10°C (Fig 1). No other treatment showed a significant effect on gastropod behaviour (Table 1). Both temperature (t=3.969, df=196, p<0.01; Fig 2) and predation risk (t=-1.985, df=196, p=0.048; Fig 2) had significant effects on the amount of *Ulva* consumed, although the interaction was not significant (t=-1.759, df=196, p>0.05; Table 1). Temperature significantly increased snail foraging (Fig 2), with a mean of 13.42% being consumed at 20°C compared to 5.73% at 10°C. The addition of predation cue caused *L. littorea* to consume significantly less *Ulva* compared to control conditions (Fig 2).

Table 1. Summary of results from analyses of time spent (a) moving, (b) eating, (c) stationary, (d) at the waterline, (e) out of the water and (f) amount of *Ulva* consumed. Temperature and treatment were fully crossed fixed effects.

Behaviour	Effect	Df	*T*	P
(a) Moving	Treatment	196	0.776	0.44
	Temp	196	-4.976	<0.0001
	Treatment x temp	196	1.296	0.20
(b) Eating	Treatment	196	-0.289	0.77
	Temp	196	0.417	0.68
	Treatment x temp	196	0.262	0.79
(c) Stationary	Treatment	196	-1.347	0.18
	Temp	196	4.410	<0.0001
	Treatment x temp	196	-1.770	0.08
(d) At the waterline	Treatment	196	1.415	0.16
	Temp	196	-0.353	0.72
	Treatment x temp	196	0.388	0.70
(e) Out of the water	Treatment	196	0.185	0.85
	Temp	196	-0.290	0.77
	Treatment x temp	196	0.377	0.70
(f) *Ulva* consumed	Treatment	196	1.985	0.04
	Temp	196	3.969	<0.01
	Treatment x temp	196	1.759	0.08

A



B

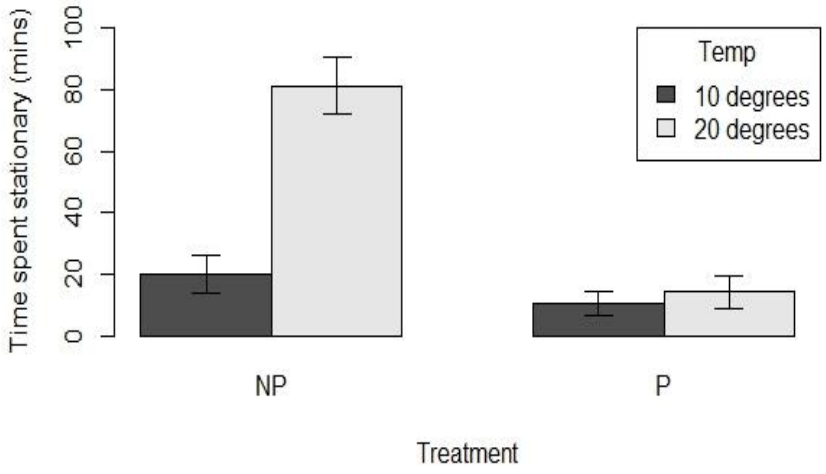


Figure 1. Mean (± SE) time spent (a) moving and (b) stationary between treatments, no predator (NP) and predator (P) and across temperatures (10 and 20 degrees).

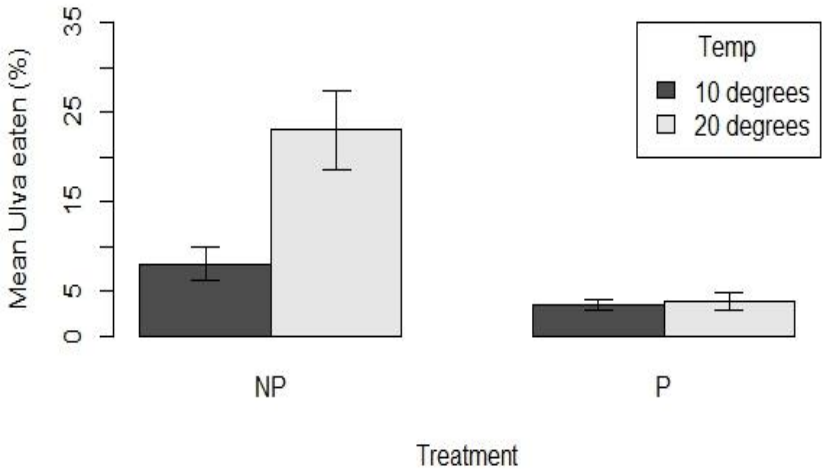


Figure 2. Mean (± SE) *Ulva* consumed between treatments, no-predator (NP) and predator (P) in different temperatures (10 and 20 degrees)

Discussion

It has been shown that periwinkles generally increase their crawling speed and activity with increasing temperature (Newell 1958), as individuals move closer to the optimal temperature of their thermal performance curve (Huey & Kingsolver 1989). However, my results are at odds with this;- an increase of ten degrees resulted in the total time spent stationary increasing, whilst cooler conditions resulted in individuals becoming more active. This suggests that the higher temperature of 20°C pushed these individuals past their optimum and into a more stressful temperature range. Mean monthly sea surface temperatures around Plymouth Sound range from 9°C in March to a maximum of 16°C in August (Smyth et al. 2010). The decrease in activity I observed at 20°C may therefore be the result of *L. littorea* trying to compensate for thermal stress. The act of withdrawing into the shell has been reported to reduce body temperature of Littorinids by up to 4°C, as it reduces the amount of heat exchange with the substrate (Miller & Denny 2011). This behavioural trait can therefore assist snails in controlling body temperature, which is particulary important for individuals approaching their thermal threshold. The increase in movement I observed at 10°C suggests that this is closer to the optimal temperature of their thermal performance curve, however, the reduced *Ulva* consumption at this temperature contradicts this hypothesis. Another explaination for this contradiction, is that the lower temperature may be stimulating migration behaviour. Previous studies (Lambert & Farley 1968; Underwood 1973; Gendron 1977) have shown that *L. littorea* migrate seasonally down shore in response to colder conditions.

Although my behavioural observations did not detect an increase in the amount of time *L. littorea* spent foraging at 20°C, I found that after 24 hrs, *L. littorina* at 20°C had consumed 2.5 times more *Ulva* than those at 10°C. This increase in consumption may be required for individuals to meet higher metabolic demands, which increase with temperature (O'Connor 2009). This has been demonstrated in a variety of marine invertebrates including, shrimp (Wyban et al. 1995), sea stars (Sanford 2002), predatory snails (Sanford 2002) and *Littorinid* snails (Newell et al. 1971). Previous

research with related *Littorina* species found that basal metabolic rates increased at temperatures ranging from 22-25°C (Newell & Northcroft 1967). Although the highest temperature in my experiments were below that of Newell & Northcroft (1967), this would corroborate the significant increase observed in consumption of *Ulva* at 20°C. Therefore, increased temperatures could enhance the foraging rates of ecotherms, offsetting the positive indirect effects of predation risk on primary producers, with important consequences for community structure (Matassa & Trussell, 2014). In my experiment, predation risk caused *L. littorea* to consume 85% less *Ulva* at 20°C. I found no significant interaction between temperature and predation risk, which suggests that temperature may only have a minor role in shaping predator-prey interactions. Despite this, it appears that *L. littorea* do trade-off energy gain for safety under warming when predation risk is high. This would therefore counteract the indirect effects of warming on the abundance of primary producers as a result of increased herbivorous grazing.

It is well established that non-consumptive effects are a strong force shaping predator-prey interactions (Morgan et al. 2016), as predator induced phenotypic plasticity can be immediate and affect individuals within a local population throughout their lifetime (Peacor & Werner 2001). My results provide further evidence that the effect of predation risk can influence the behaviour of prey. I found that the addition of predator cue caused *L. littorea* to consume 77% less *Ulva* compared with control treatments, resulting in a positive indirect effect on *Ulva*. These risk specific differences in the impact of their food rescource likely reflect predator induced changes in snail behaviour. Marine gastropods frequently respond behaviourally to the presence of predators (Jacobsen & Stabell 1999). For example, aquatic snails climb to the water surface as a behavioural response to crayfish and *Belostoma* predators (Alexander & Covich 1991; Covich et al. 1994; Turner 1996). Furthermore, Yamada et al. (1998) reported how *Littorina sitkana* changed their behaviour by climbing above the water level in cages in the presence of predatory crabs that were actively feeding on conspecific snails. In contrast to these studies, I did not observe an increase in anti-predator behaviour. The sampling interval and duration of my behavioural observations may have been inadequate to detect the change in behaviour responsible for the measured changes in consumption. Wojdak (2004) reported that snails showed little immediate response to predation cues. Reductions in foraging and increased refuge use was only observed 19 hours after predators had killed snail prey. In the present experiment, behaviour was only observed for the first 150 minutes. If I had observed behaviour over a longer period, I may have witnesed the expected anti-predator behavioural response to predation risk. Alternatively, *L. littorea* may have preferred to vertically migrate in the dark than in the light. This may be an adapated form of anti-predator behaviour that has evolved in response to night active predators, such as crabs, that have been shown to migrate to the upper intertidal at high tide during night hours (Jacobsen & Stabell 1999). Vertical migration in the dark has been documented for several gastropods (Rogers 1968; Phillips 1975). For example, Jacobsen & Stabell (1999) demonstrated that experiments carried out in the dark resulted in a higher proportion of *L. littorea* leaving the water compared to experiments in the light. This form of anti-predator behaviour would be consistent with the diminshed impact on the snails food resource.

Conclusion

This study shows that the effects of temperature and predation risk can both independently elicit behavioural responses in *L. littorea.* Despite no interaction between these two stressors it appears that *L. littorea* do trade energy gain for safety when predation risk is high. This demonstrates that foraging under predation risk involves a trade-off between benefits gained from feeding and costs of increased vulnerability to predation. My results highlight the complex ways TMIs and environmental stressors may influence predator-prey interactions as well as having cascading effects on their primary resources. They additionally support the argument for incorporating non-consumptive effects and the effects of temperature change into the study of food-web dynamics (Peacor and Werner 2001) in order to comprehensively estimate cascading impacts of predation on communities, particularly in habitats that experience fluctuating levels of sea and air temperature, such as the rocky shore.

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